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番荔枝科研究 35. *Guatteria* 类群和有关属的系统发育

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摘要 *Guatteria* 类群由 4 个新热带的属组成，即 *Guatteria*，*Guatteriopsis*，*Guatteriella* 和 *Heteropetalum*。不同的作者基于不同的证据得出的它在番荔枝中的地位各不相同。基于宏观和微观的形态特征，对该类群进行了表型和分支分析。分支分析表明，所研究属的系统发育分支方式仅由极少数共同衍征支持，同型现象非常明显，所获得的唯一的最简约分支图可分为两个基本部分，即一个（假）合生心皮分支和一个离生心皮 grade。在表征聚类图和主成分分析的三维构象图中同样可以区分出离生心皮和（假）合生心皮两个表征群，表征分析表明 *Guatteria* 类群处在其它离生心皮类和（假）合生心皮类的中间位置。然而分支分析表明 *Guatteria* 类群与番荔枝科中最进化的（假）合生心皮类有姊妹群关系。*Guatteria* 类群是离生心皮类中最进化的一类。番荔枝科中离生心皮类和（假）合生心皮类在漫长的进化过程中经历了强烈的形态分化而显示出极大的形态差异，然而在系统发育上它们可以通过 *Guatteria* 类群作为纽带而联系起来。

关键词 *Guatteria* 类群，番荔枝科，系统发育
分类号 Q 941

Studies in Annonaceae. XXXV. Phylogeny of the *Guatteria*-group and Related Genera

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Abstract The *Guatteria*-group consists of four neotropical genera, *Guatteria*, *Guatteriopsis*, *Guatteriella*, and *Heteropetalum*. Its systematic position within Annonaceae, interpreted by different authors based on various sources of evidence, is quite questionable. In this paper phylogenetic and phenetic analyses were carried out by using 44 phylogenetically informative characters from morphology, leaf and wood anatomy, as well as palynology of 38 annonacaeous genera with Magnoliaceae as outgroup. The phylogenetic analysis indicates that the phylogeny of selected genera in Annonaceae is weakly supported with branching patterns determined by few, mostly homoplasious, characters. Homoplasy in the studied genera is pervasive. The single most parsimonious tree obtained can be divided into two basic parts, i.e., a (pseudo)syncarpous

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clade and an apocarpous grade. The corresponding two phenons, i.e., the apocarpous vs. (pseudo)syncarpous ones, are also recognized in the phenogram and in the three-dimensional plot of the first three principal coordinates. On the base of our data set, the phenetic analyses agree broadly with the view of van Setten & Koek-Noorman (1992) that the *Guatteria* -group takes an intermediate position between other apocarpous genera and the (pseudo)syncarpous genera. Our phylogenetic analyses strongly suggest a sister group relation of the *Guatteria* -group with the most derived (pseudo)syncarpous genera in Annonaceae. It also indicates that the *Guatteria* -group is the most derived one among the apocarpous genera. Though the apocarpous and the (pseudo)syncarpous genera have undergone drastic morphological divergence in the long history and thus exhibit high superficial dissimilarities, they can possibly be related to each other phylogenetically via the *Guatteria* -group as a link.

Key words *Guatteria* -group, Annonaceae, Phylogeny

The pantropical family Annonaceae, one of the most primitives of the angiosperms, represents a morphologically well – defined group (Fries, 1959) which can be clearly delimited from its closest relatives, such as Myristicaceae, Eupomatiaceae (Uphof, 1959), and Magnoliaceae (Hutchinson, 1964; Kessler, 1993; Nooteboom, 1985, 1993). Nevertheless, the ca. 2000 known annonaceous species (van Setten & Maas, 1990) exhibit the most diverse range of pollen types, floral morphology, and habit. Such extensive variation and differentiation as well as the high number of species make the subdivision of the family particularly difficult (Sinclair, 1955; Schatz & Le Thomas, 1993; Kessler, 1993). The enormous amount of reticulate distribution of primitive and advanced characters as well as parallelism make it difficult to assess the evolutionary relationships among the genera and to establish the monophyletic tribes which are comparable end products of the evolutionary process (Kessler, 1993). The reticulate nature of character expression has confounded the elucidation of relations among the genera and has resulted in largely artificial groupings based on often ambiguous criteria, e.g., establishment of the subfamilies and tribes on aestivation and inflorescence position (Sinclair, 1955; Fries, 1959; Hutchinson, 1964). Informal groupings of genera were described on pollen features (Walker, 1971 a, b), and on combinations of floral characters (van Heusden, 1992) as well as of fruit characters (van Setten & Koek-Noorman, 1992).

Despite the notable disagreement by different authors on the infrafamilial division, some genus – groups, such as the *Annona-*, *Guatteria-*, and *Cymbopetalum* -group, have been recognized for a long time by their highly homogeneous flower and fruit characters as well as by other features (pollen structure, base chromosome numbers).

One of the homogeneous genus-groups just mentioned is the *Guatteria* -group consisting of *Guatteria*, *Guatteriopsis*, *Guatteriella*, and *Heteropetalum*. All four genera are neotropical. This group represents about 10% of all annonaceous species and includes the largest genus *Guatteria* (ca. 250 spp.,) of the family (van Setten & Koek-Noorman, 1992). The *Guatteria* -group is characterized by valvate sepals, imbricate to valvate petals, one basal ovule per carpel, and numerous carpels and stamens. The stamens are indurate (somewhat lignified) and the margins of the slit of the thecae are usually inflexed. Also in non-floral features this is a coherent group, e.g., in their almost stable

micromorphological characters within the group (chromosomes, pollen, leaf surface) (Morawetz & Waha, 1985). *Guatteriella* and *Guatteriopsis* in their flowers are very close to *Guatteria*. *Heteropetalum* deviates from the other three genera in the difference in size between inner and outer petals, the slightly different stamens (less indurate in texture and the margins of the slit of the thecae not inflexed when dehiscing), and the different shape of the stigma (van Heusden, 1992).

Sharply contrasting to the unambiguous circumscription of the *Guatteria* -group is the strong debate concerning its phylogenetic relationship with other genera in the family. Within the framework of Fries's classification, largely based on floral morphology, the *Guatteria* -group belongs to the most primitive annonaceous tribe, the Uvarieae. It is placed by Fries (1959) after his *Uvaria*-, *Duguetia*- (including *Malmea*), *Asimina*-, and *Hexalobus* -groups, suggesting that it is the most advanced group within the Uvarieae. The four genera are also grouped in the informal *Guatteria* -tribe on palynological grounds (Walker, 1971a, b). In Walker's scheme, the *Guatteria* -tribe appears after the *Malmea* - and *Uvaria* -tribes, constituting the *Malmea* -subfamily, which is considered primitive, and in this sense agree broadly with Fries's system.

Recent character analyses point toward different nearest relatives of the *Guatteria* -group. According to van Heusden (1992), the *Guatteria* -group shows most similarity with her *Fusaea* -group: both have the same aestivation of sepals and petals, indurate stamens, and one basal ovule. It also resembles the *Cremastosperma* -group based on the fact that the size of the flowers is similar, both groups have one basal ovule per carpel, and the same number of stamens and carpels. According to van Setten & Koek-Noorman (1992), however, the *Guatteria* -group takes an intermediate position between the *Duguetia*-, *Annona*- and *Cremastosperma* -groups.

Morawetz & Waha (1985) suggest that the group occupies a somewhat isolated position in Annonaceae because of its distinct pollen type (zonoaperturate with a folded aperture region and an extremely reduced exine), its unusual chromosome differentiation mode, and some of its cuticular folding patterns.

The clustering analyses of a combined data set of flowers, fruits and seeds indicate that the *Guatteria* -group is closely related to the (pseudo)syncarpous genera (Koek-Noorman *et al*., 1997), while in the cladistic analysis of Doyle & Le Thomas (1994), the syncarpous *Annona* -group and pseudosyncarpous *Duguetia* -group are found well apart in separate clades.

van Zuilen *et al*. (1996) carried out a phylogenetic analysis of morphological and molecular data, but concentrated on the (pseudo)syncarpous genera and left out the *Guatteria* -group.

The interpretation of the position of the *Guatteria* -group by different authors, based on various sets of characters and methods, thus seems to be quite questionable. So the goal of the present study is to assess the phylogenetic relationship of the *Guatteria* -group.

Materials and methods

We adopted the principles of phylogenetic systematics as originally developed by Hennig (1966),

who stressed that only strictly monophyletic taxa can be regarded as historical entities and that the logical basis for inferring monophyly is to show that the components of a group possess one or more shared, derived character states or synapomorphies. On the basis of these synapomorphies, taxa are combined into one or more hierarchical sets represented by branching diagrams. The principle of parsimony is employed in choosing among the numerous hypotheses generated. For comparision, we used the same data set with outgroup excluded for two phenetic analyses, viz., the cluster analysis and the pricipal coordinate analysis.

Choice of the terminal taxa

The terminal taxa chosen for the analysis (Table 1) are: (1) *Guatteria*, *Guatteriella*, *Guatteriopsis*, and *Heteropetalum* which form the *Guatteria* -group; (2) the genera *Duckeanthus*, *Duguetia*, *Fusaea*, *Letestudoxa*, *Pachypodanthium*, and *Pseudoartabotrys* which form group 1 (*Duguetia* -group) sensu Koek-Noorman *et al*. (1997); (3) the four genera of the *Annona* -group, *Annona*, *Anonidium*, *Raimondia*, and *Rollinia*; (4) 12 genera of group 4, and nine genera of group 10 sensu Koek-Noorman *et al*. (1997); (5) *Anaxagorea*, and (6) *Uvaria* and *Cymbopetalum* representing groups 16 and 6 sensu Koek-Noorman *et al*. (1997) respectively.

The choice of the terminal taxa in the cladistic analysis was mainly based on the following arguments. The phenetic analysis of 125 genera of Annonaceae, based on 311 morphological characters, strongly suggests a close relationship of the *Guatteria* -group with groups 1 (*Duguetia* -group), 2 (*Annona* -group) and 4 (*Cremastosperma* -group), and also tends to be with group 10 (Koek-Noorman *et al*., 1997). *Anaxagorea*, a very distinct genus in Annonaceae (Maas & Westra, 1984), is also included because we intend to test its basal position in the family (Doyle & Le Thomas, 1994; van Zuilen *et al*., 1996). Two more genera, namely, *Uvaria* representing the *Uvaria* -group and *Cymbopetalum* of the *Cymbopetalum* -group, are also included because phylogenetic studies based on combined characters from morphological, molecular, palynological, and cytological researches indicate that the *Guatteria*- group is more or less related to the *Uvaria*- and *Cymbopetalum*- groups (van Zuilen *et al*., 1996). Doyle & Le Thomas (1994), in their analysis, also found close relations between *Uvaria*, *Cymbopetalum*, and the (pseudo)syncarpous genera.

Outgroup selection

Magnoliaceae are generally considered as closely related to the Annonaceae (Hutchinson, 1969; Kessler, 1993; Nooteboom, 1985, 1993), and this family was therefore selected as outgroup for our analysis. Both families are woody, have three lacunar nodes, entire leaves, numerous, spirally arranged stamens, and numerous free carpels, as well as the same pollen type. Some genera, e.g., *Liriodendron*, have the same floral formula as most genera in Annonaceae (Doyle & Le Thomas, 1994). Annonaceae differ from Magnoliaceae in their lack of stipules, their ruminate endosperm, and their possession of sepals and usually two distinct whorls of three petals each vs. the spiral insertion of an indeterminate number of tepals, and their usually convex as opposed to an elongate receptacle. The occurrence of the fine continuous apotracheal tangential bands of parenchyma is another unique character sufficient to differentiate Annonaceae from all other closely related families including Magnoliaceae

(ter Welle, 1984). The dehiscent carpels of *Anaxagorea* remind of Magnoliaceae. Some genera in Annonaceae, e.g., *Toussaintia* and *Mischogyne*, however, exhibit elongate receptacles, in effect androgynophores, with numerous stamens spirally inserted. The stamens of *Mischogyne michelioides* Exell are extremely aberrant within Annonaceae consisting almost entirely of anthers that lack the characteristic apical connective prolongation and closely resemble those of *Michelia* in Magnoliaceae (Schatz & Le Thomas, 1993).

Table 1 Acronyms, estimated numbers of species, geographic distribution of the studied genera and their previous grouping in Annonaceae (Magnoliaceae as outgroup)

Genus	Acronym	Estimated No. of species	Geographical distribution
Magnoliaceae	MAGN	160	Temperate and tropical SE, E Asia; N America through West Indies and Central America to S Brazil
Anaxagorea	ANAX	27	Tropical America and tropical E Asia
Duckeanthus	DUCK	1	NW Brazil
Duguetia	DUGU	85	Tropical S America, a few in central America
Fusaea	FUSA	2	Tropical S America
Letestudoxa	LETE	2	Tropical W Africa
Pachypodanthium	PACH	3	Tropical W Africa
Pseudartabotrys	PSEA	1	Gabon
Annona	ANNO	115	Tropical America and tropical W Africa
Anonidium	ANON	5	Tropical Africa
Raimondia	RAIM	5	Colombia and Ecuador
Rollinia	ROLL	44	Tropical S America, a few in West Indies, Mexico and Central America
Guatteria	GUTA	250	Tropical America
Guatteriella	GUTE	2	Amazonian Brazil
Guatteriopsis	GUTO	4	Tropical S America (Amazon region)
Heteropetalum	HETE	1	NW Brazil and S Venezuela
Enicosanthum	ENIC	16	Ceylon, Burma, Thailand, Malayan Peninsula, Borneo, the Philippines
Ephedranthus	EPHE	4	Tropical S America
Malmea	MALM	30	Central and tropical S America
Neouvaria	NEOU	2	Indo-Malaya
Oxandra	OXAN	22	Tropical America
Phaeanthus	PHAE	12	Lower Burma to the Philippines
Pseudephedranthus	PSEE	1	N Brazil and Venezuela
Ruizodendron	RUIZ	1	W and SW tropical S America
Trivalvaria	TRIV	5	Indo-Malaya
Woodiellantha	WOOD	1	Sarawak, Brunei and Sabah of Borneo
Cremastosperma	CREM	17	Tropical S America, a few in Central America
Pseudoxandra	PSEO	6	Guyana and Brazil
AfroGuatteria	AFRO	2	Angola and Congo
Dasymaschalon	DASY	15	E Asia, the Philippines and Sunda Islands

续表 1

Genus	Acronym	Estimated No. of species	Geographical distribution
Desmos	DESM	30	Assam to S China and the Philippines
Disepalum	DISE	6	Malayan Peninsula, Borneo Sumatra
Friesodielsia	FRIE	60	Tropical Asia, a few in Tropical W Africa
Gilbertiella	GILB	1	Zaire
Monanthotaxis	MONA	45	Tropical Africa and Madagascar
Sphaerocoryne	SPHA	9	Tropical SE Asia; E and SE Africa; Madagascar
Schefferomitra	SCHE	1	New Guinea
Uvaria	UVAR	110	Old World tropics including Queensland
Cymbopetalum	CYMB	27	Mexico, Central and tropical S America

Table 2 Characters scored for the phylogenetic and phenetic analyses of the systematic position of the *Guatteria*- group. All multistate characters are unordered. The morphological characters except those specifically referenced were scored from Sinclair (1955), Fries (1959), Le Thomas (1969), Verdcourt (1971), Huber (1985), Maas *et al*. (1983), Kessler (1993), van Heusden (1992), van Setten & Koek-Noorman (1992), and our observations.

1. Habit: tree/shrub (0), liana/lianescent (1).
2. Primary vein on adaxial side: concave/flat (0), convex (1). Huber (1985); van Setten & Koek-Noorman (1986); Scheffer (1885), Diels (1912) for Schefferomitra; Merrill (1922) for Woodiellantha; Pierre (1880) for Sphaerocoryne (= Unona mesnyi); our observations.
3. Histology of primary vein: simple arc (0), arc plus adaxial plate (1), complex, with phloem and/orsclerenchyma intruding xylem body (2). Jovet-Ast (1942); Sugiyama (1979); Metcalfe (1987); van Setten & Koek-Noorman (1986).
4. Secondary veins: strongly to moderately curved (0), straight/slightly curved (1). Klucking (1986);Morawetz & Maas (1984) for Guatteriella; Westra (1995) for Raimondia; Fries Duckeanthus; King (1893), Pierre (1880) for Sphaerocoryne; our observations.
5. Tertiary veins: reticulate (0), percurrent (1). Klucking (1986).
6. Indument: simple/absent (0), stellate and/or lepidote (1).
7. Number of vessels per mm^2: >40 (0), 10~40 (1), <10 (2). B. J. H. ter Welle (unpub. data).
8. Parenchymatic sheath surrounding the vessels: absent/incomplete (0), one cell wide (1), two cells wide (2). B. J. H. ter Welle (unpub. data).
9. Inflorescence: terminal (leaf-opposed, supra-axillary, etc.) (0), axillary (1). Aristeguieta (1969) for Pseudephedranthus; our observations.
10. Bracts: 0~3 per flower (0), >3 (1). Scheffer (1885), Diels (1912) for Schefferomitra; Aristeguieta(1969) for Pseudephedranthus; our observations.
11. Fusion of sepals: free (0), fused (at least basally) (1).
12. Sepal aestivation (in bud): imbricate (0), valvate (1). Scheffer (1885), Diels (1912) for Schefferomitra.
13. Sepal size: >10 mm (0), 5~10 mm (1), <5 mm (2).
14. Petal aestivation (in bud: outer whorl if two whorls differ): imbricate (0), valvate (1). Pierre (1880)for Sphaerocoryne (= Unona mesnyi).
15. Petals: free (0), fused (at least basally) (1). Pierre (1880) for Sphaerocoryne (= Unona mesnyi).
16. Petals or tepals: ≥two whorls, subequal (0), two whorls, unequal (1), one whorl (2).
17. Petal length/sepal length ratio: <5(0), >5(1).

续表 2

18.	Petal length/width ratio < 3 (0), > 3 (1). Pierre (1880) for Sphaerocoryne (= Unona mesnyi); Fries(1934) for Duckeanthus; Aristeguieta (1969) for Pseudephéranthus; Ban (1975), Finet & Gagnepain (1906) for Dasymaschalon.
19.	Staminodes: absent (0), present (1).
20.	Stamen morphology: laminar (0), with conical to tongue-shaped connective (1), with truncate dilatedconnective (cap concealing anthers) (2), without prolonged connective (3).
21.	Texture of stamen: fleshy (0), indurate (1).
22.	Margin of thecae turn outwards upon dehiscence (0), turn inwards (involute) (1).
23.	Anthers: introrse (0), latrorse (1), extrorse (2).
24.	Pollen unit: single (monads) (0), compound (tetrads, polyads) (1).
25.	Pollen size (average): small (< 45μm) (0), medium (1), large(> 90μm) (2).
26.	Pollen shape: elongate (boat-shaped) (0), globose (1).
27.	Exine: normal (0), reduced (1).
28.	Aperture: sulcate (0), inaperturate (1), sulculate (2). Character 24 ~ 28, Walker (1971a, b, 1976); Le Thomas & Lugardon (1974); Le Thomas (1980 ~ 1981).
29.	Receptacle: elongate (0), convex/flat (1), concave (2).
30.	Stigma: sessile (0), capitate (base strongly constricted)(1), with elongate style (2).
31.	Ovules per carpel: numerous (> 5) (0), 2 ~ 5 (1), one (2).
32.	Placentation of ovules: lateral/apical (0), basal (1).
33.	Fruit: apocarpous (0), pseudosyncarpous (1), syncarpous (2).
34.	Base of monocarp: sessile/very short stipe (0), stipitate (1).
35.	Number of monocarps (maximum number developing): > 30 (0), 15 ~ 30 (1), < 15 (2).
36.	Basal collar: absent in apocarpous fruit (0), absent in syncarpous fruit (1), formed from remnants of calyx, torus, or receptacle (2), from sterile carpels (3).
37.	Dehiscence of monocarps: dehiscent (0), indehiscent (1).
38.	Fruit wall: thick (> 1.5 mm) (0), thin (< 1.5 mm) (1).
39.	Raphe: a groove (0), not manifest/flat/indistinct rib (1), distinct rib (2).
40.	Endosperm: normal (0), glass-like/stony (1).
41.	Oil cells in endosperm: present (0), absent (1).
42.	Seed surface: smooth to finely transversely striate (0), foveolate/scrobiculate (1).
43.	Aril: absent (0), rudimentary (1), lobed/ring-shaped (2).
44.	Ruminations: absent (0), lamellate (1), spiniform/peg-shaped (2).

Character definition and coding

Data from 44 characters were derived from morphology, anatomy, and palynology (table 2). Character polarity was determined by the outgroup comparison method (Humphries & Funk, 1984; Maddison *et al.*, 1984; Watrous & Wheeler, 1981). According to this method, when a character varies within a group, the state occurring in the related group (outgroup) is assumed to be plesiomorphic. All multistate characters were unordered. Table 3 contains the data matrix used in the analysis.

Despite the large amount of systematic data available for the family, we were able to generate only 44 phylogenetically informative characters. The non-informative characters that were excluded from this study fall into four categories: 1). autapomorphies for a single genus studied (e.g., calyptrate sepals

Table 3 Data matrix (Acronyms: see table1). a = 0/1, b = 1/2, ? = unknown

	1 2 3 4 12345678901234567890123456789012345678901234
MAGN	001000a0a00000000000000a00000a0000000?00000
ANAX	00100a1010a1110a1a1000b0100010110?1001101012
DUCK	01?0001100010001000210b121012221101211101011
DUGU	0000011000a1000a0002002011112221100311111011
FUSA	00201011001100a11012102121012221200210101011
LETE	10?000??001100010002112011022221200311101011
PACH	00210122a0010000000200200101b221b?0310201021
PSEA	10?100??000101001002112021012221200211200011
ANNO	00100abb0011b1aa0a0200212111b12120011a101a1b
ANON	00200022001aa1000a0200212111112120011a201011
RAIM	000aa01200a121110003002111111121200111100a12
ROLL	001a0abb00a12111000200201111b121b0011a100a1b
GUTA	0020002211a1a00a00021120111221210100111a111b
GUTE	00201022111111000002112011122121011011101101
GUTO	0020002211011100000211201012212101101110100b
HETE	00200022110111011002102010121121002011001101
ENIC	00?1102010001000000200200101112101101a001001
EPHE	00011010110020000000200201000102101001001001
MALM	0 a000010a0a02000000200201000112101001aba111b
NEOU	00?111??1011210a100200b0010110210a201a00a001
OXAN	0a0000001000200001010020000010210a2011aa010b
PHAE	000aa0100001b1010a020020110110210110110100b
PSEE	01?000??11102000010100200000010210a2011000001
RUIZ	012100??10102000010200200000102001201101001
TRIV	00?11011000a2a0a1002002011011021011011100100b
WOOD	00?100??0011b11000020020010110210100110000 01
CREM	0100000010a0200000002002010002b20011011a11102
PSEO	010000101a00200a0002002110001120012011a11102
AFRO	10?000??0001100a0002001001111a2101001a100001
DASY	000110??a0a1a102000200200a011a10011011100001
DESM	1000a00?00a1a1010a0200200100ba1001001110a001
DISE	00000021000111120a0200212a0020b101001110a001
FRIE	10?1101?0011a1010a0200200101b0b0010011100001
GILB	10?1101?a011210b000100200101100001201110 1001
MONA	a0?11012001121ab1a0300b0010110a0011011100001
SPHA	00?000??10112101000200200101101001101110 0001
SCHE	1 0?110??101121011001002001 01?02001101110 0001
UVAR	a00a01010011a0aa001210b01111100001001a200a1b
CYMB	0100001000012101100200212111100001100a101021

in *Letestudoxa*; locellate anthers and boat-shaped inner petals in *Cymbopetalum*; the dorsal wing in

outer petals of *Rollinia*; the glandular dots on stamens of *Oxandra*) because these do not indicate phylogenetic relationships; 2). synapomorphies for the whole family (as already discussed under outgroup selection); 3). characters that are known to vary strongly within genera, e.g., many leaf anatomical characters like most features surveyed by van Setten & Koek-Noorman (1986), showing extensive variation that is useful diagnostically but difficult to incorporate in a cladistic analysis; 4). Characters incompletely known, unreliably described, or the homology of which is disputed, were omitted. For instance, most cytological and pollen ultrastructural features may be of phylogenetic significance, but sources are of varying reliability and information for the studied genera is too fragmentary to be included. Some macromorphological characters, such as floral type defined by Morawetz (1988) and base of petals, also fall into the same category to be excluded.

Data analysis

Phylogenetic analyses were undertaken with the PAUP program (Swofford, 1993) version 3.1.1 for Apple/Macintosh. In order to find the most parsimonious trees, the heuristic searches were performed with Tree-Bisection-Reconnection (TBR) branch swapping on 100 starting trees, built with simple addition sequence and with steepest descent. MacClade (Maddison & Maddison, 1992) version 3.0 was used to study the character evolution.

The same data set, with outgroup excluded, was further applied for a phenetic analysis with the help of NTSYS-pc (Rohlf, 1994) version 1.8. For a cluster analysis, the sub-program SIMQUAL was used to compute the Rogers-Tanimoto association coefficient matrix which was then clustered by UPGMA with the sub-program SAHN. The clustering result by SAHN was displayed as dendrogram by using the sub-program TREE. The data set was used again in SIMQUAL to compute the simple matching association coefficient matrix which was further double-centred by a sub-program DCENTER. The resulting data matrix was caculated by EIGEN to produce the eigenvalues and eigenvectors which were then used in a principal coordinate analysis by the sub-program PROJ. Output of PROJ was used to produce a three-dimensional plot of the first three principal coordinates by processing a sub-program MOD3D. A minimum spanning tree produced from the above mentioned association coefficient matrix by the sub-program MST was superimposed on the three-dimensional plot.

Results and discussion

The heuristic search with simple addition sequence yielded a single most parsimonious tree of 216 steps (fig. 1), with a consistency index (CI) of 0.296, a retention index (RI) of 0.611, and a rescaled consistency index (RC) of 0.181. The homoplasy index (HI) is 0.704, which indicates the homoplasy in the studied genera is pervasive. Though the relatively large number of taxa in the study is influential in raising the amount of homoplasy in the analyses (Sanderson & Donoghue, 1989), the variation of the morphological characters employed has contributed largely to the complexity of the cladogram. The phylogeny of selected genera in Annonaceae is weakly supported with branching patterns determined by few, mostly homoplasious, characters.

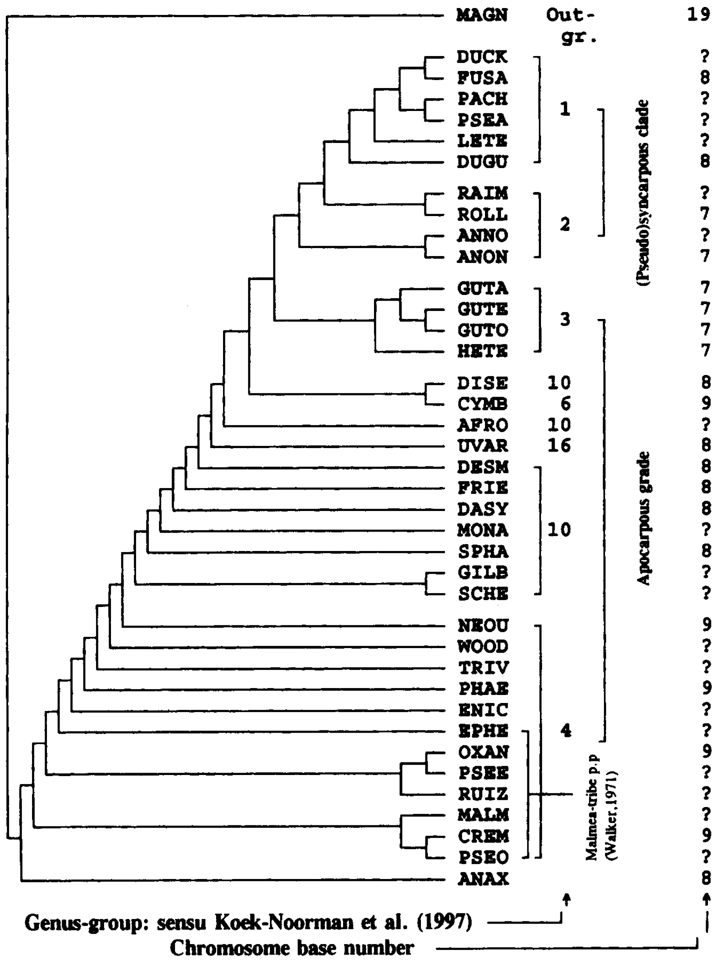

Figure 1 The single most parsimonious tree of the *Guatteria* -group and its related genera, using Magnoliaceae as outgroup [length = 216, consistency index (CI) = 0.296, retention index (RI) = 0.611, and rescales consistency index (RC) = 0.818]. Number of the genus groups sensu KOEK-NOORMAN *et al*. (1997) and the chromosome base numbers were overlaid on the tree.

The cladogram can be divided into two basic parts, i.e., an upper (pseudo) syncarpous clade and a lower apocarpous grade. The corresponding two phenons can be recognized in the phenogram based on Rogers-Tanimoto association coefficients clustered by UPGMA (fig.2) and in the three dimensional plot of the first three principal coordinates (fig.3).

Most species of Annonaceae have apocarpous fruits, with the individual carpels termed monocarps. The number of monocarps varies from low to high, as does the number of ovules. We accept the results by van Heusden (1992), van Setten & Koek-Noorman (1992), van Zuilen *et al*. (1996) and Leins & Erbar (1996), that the fruits of *Isolona* and *Monodora* are single monocarps, where the placentation changed towards laminar. Besides these fruits, there are the so-called (pseudo) syncarpous fruits resulting from the complete or incomplete fusion of closed carpels as those in the *Duguetia*- and *Annona*- groups. Schatz & Le Thomas (1993) questioned whether genera sharing such (pseudo)syn-

carpous fruits are actually closely related or merely examples of convergence under selection for probable dispersal by large vertebrates. They concluded that the (pseudo)syncarpous genera have originated

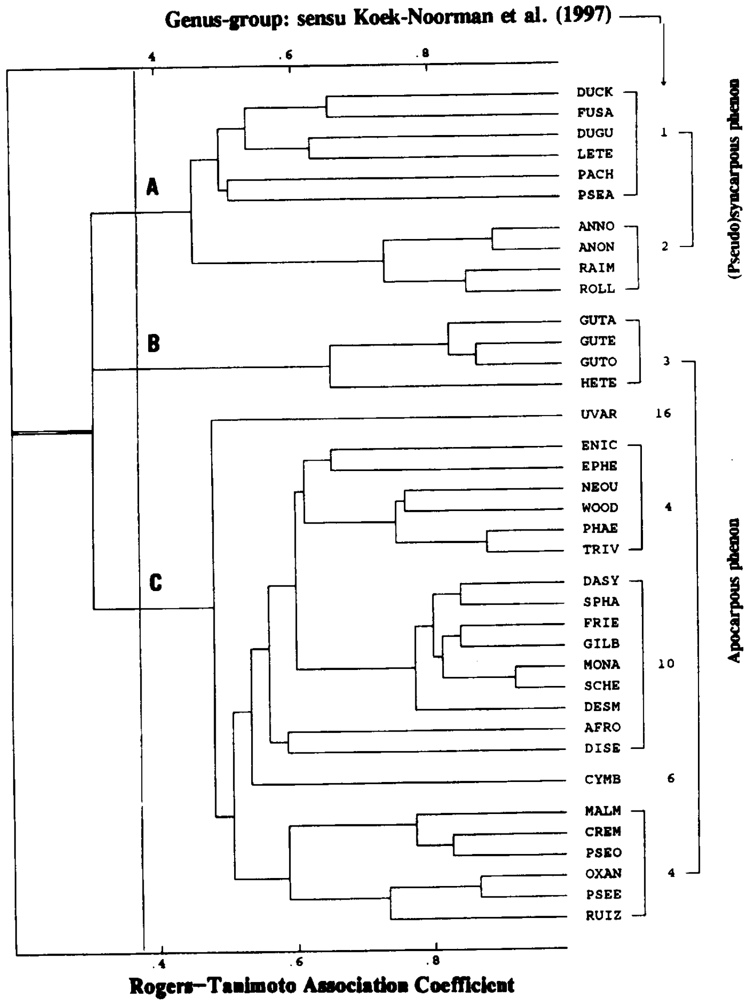

Figure 2 Phenogram generated from the same data set, with outgroup excluded, of the *Guatteria* -group and related genera as in the phylogenetic analysis, using Rogers-Tanimoto association coefficients which are clustered by UPGMA.

several times independently and thus were not a monophyletic group. Sharply contrary to their conclusion is the suggestion by Kessler (1993) who unites all the (pseudo)syncarpous genera into a broader, informal *Annona* -group. In our cladogram, the (pseudo)syncarpous genera tend to be a monophyletic clade supported by one unique synapomorphy: the presence of the (pseudo)syncarpous fruits. It is also supported by the presence of rudimentary arils [except *Pachypodanthium* (PACH) with ring-shaped aril] which are otherwise seen in *Anaxagorea* (ANAX), *Malmea* (MALM), *Uvaria* (UVAR) and *Guatteria* (GUTA) in the apocarpous grade. The *Duguetia*- group (group 1) in the (pseudo)syncarpous clade is a monophyly supported by three synapormorphies, sepals larger than 10 mm, flowers with elongate styles and fruits with basal collar. Despite its syncarpous fruits without basal collar, the

Annona- group (group 2 sensu Koek-Noorman *et al*., 1997) in the (pseudo)syncarpous clade is surprisingly paraphyletic by the fact that *Annona* and *Anonidium* together are separated from *Raimondia* and *Rollinia* .

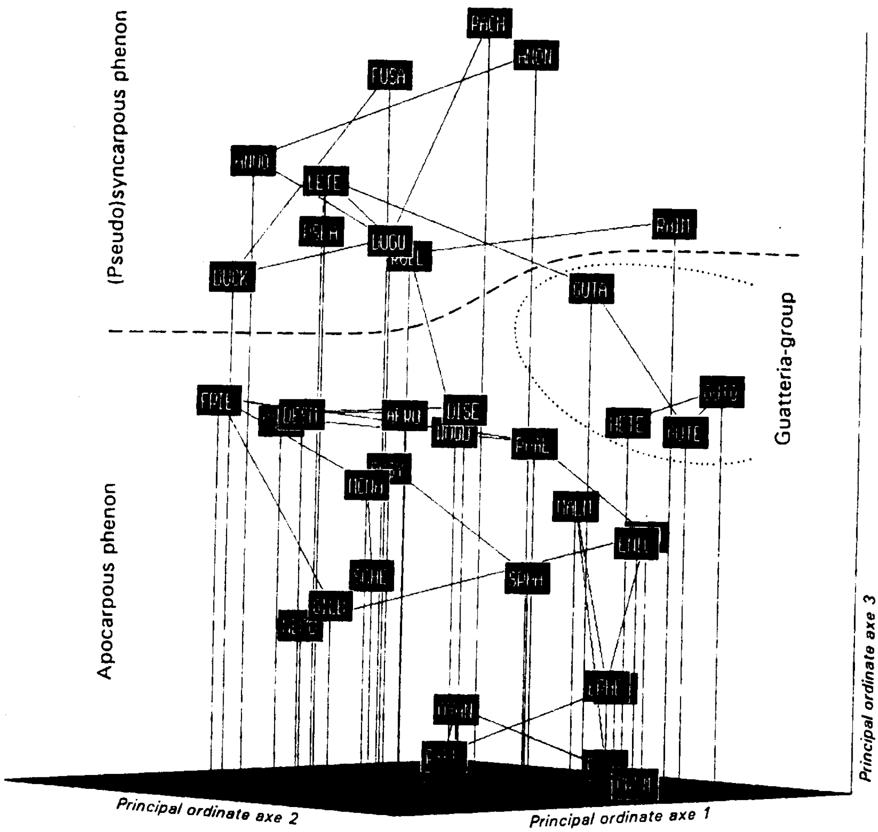

Figure 3 The three-dimensional plot of the first three principal coordinates resulted from the principal coordinate analysis of the same data set, with outgroup excluded, of the *Guatteria* -group and related genera as in the phylogenetic analysis. A minimum spanning tree was superimposed on the plot.

The apocarpous grade exhibits a more complicated branching pattern. We can not find any synapormorphies to define it. The homoplasy is extremely high in group 4 and 10 and their phylogeny tends to be a kind of mosaic, reticulate evolution pattern. Both group 4 and 10 are polyphyletic though genera from the same group come together in the cladogram. In the apocarpous grade we can find few monophyletic genus groups like the sub-basal *Oxandra* (OXAN) Ruizodendron (RUIZ) clade which is supported by one unique synapormorphy: petal length/width ratio of more than 3.

Another unambiguous result is the further confirmation of the basal position of the genus *Anaxagorea* (Doyle & Le Thomas, 1994; van Zuilen *et al*., 1996). Walker (1971a) considered the *Malmea* -tribe as the most primitive one, particularly so the genus *Pseudoxandra*. Our cladogram confirms this idea, although the seven included genera form a polyphyletic grade. It is interesting that the branching pattern of the *Malmea* (MALM)- *Pseudoxandra* (PSEO) grade in our cladogram is ex-

actly the same as that in the single most parsimonious tree found in the RFLP analysis of PCR-amplified fragments (van Zuilen *et al.*, 1996).

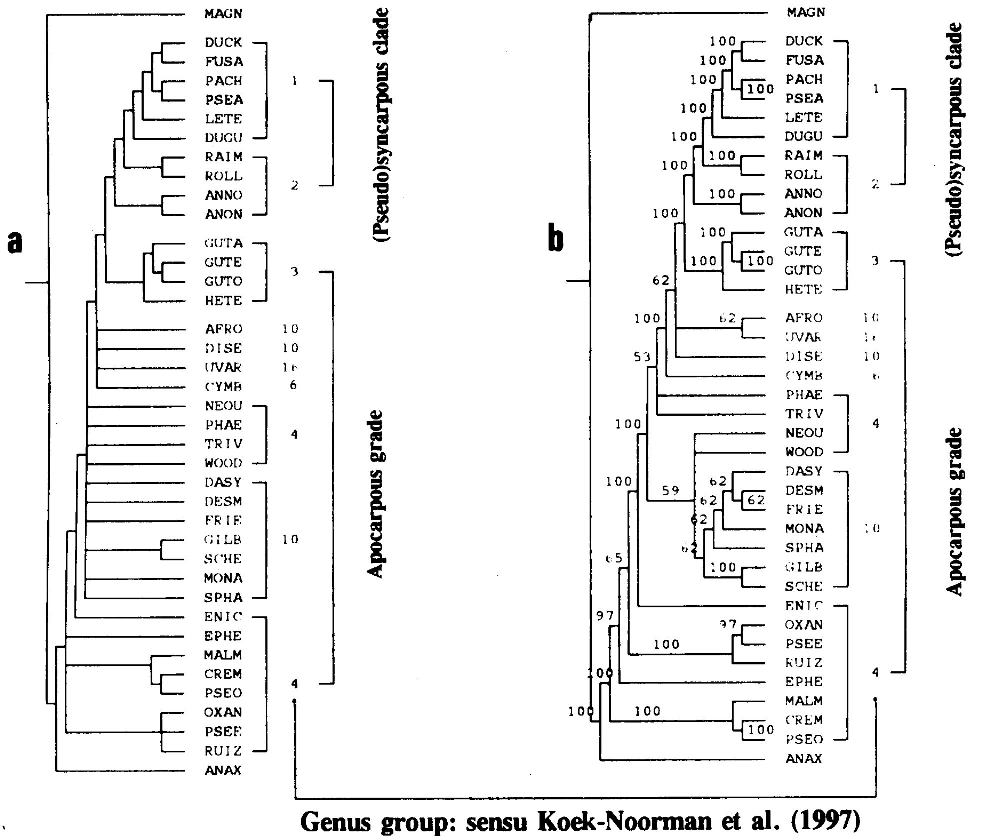

Fig 4　Strict consensus tree (a) and majority rule consensus tree (b) of 34 trees found with 217 steps.

In both strict and majority rule consensus trees of 34 trees with one step longer (fig. 4), the branching patterns of the (pseudo)syncarpous clade remains the same as that in the single most parsimonious tree. We want to emphasize the fact that in the majority rule consensus tree (fig. 4b) all branches in this clade have 100% bootstrap values, which is very convincing. The resolution is relatively low for the apocarpous grade in the strict consensus (fig. 4a) based on the fact that three polychotomies occurred. From both consensus trees, the genus groups 4 and 10 are unambiguously polyphyletic.

The systematic position of the *Guatteria*-group

The monophyly of the *Guatteria*-group is actually supported by some synapomorphies that show, however, homoplasy, like the presence of sulculate pollen apertures which is otherwise seen only in *Letestudoxa* (LETE) in the (pseudo)syncarpous clade, and the presence of more than three bracts per flower which are also found in *Ephedranthus* (EPHE) and *Pseudephedranthus* (PSEE). Its monophyly is further supported by some other cytological features not used in the present analysis, e.g., its unusual chromosome differentiation indicating a high degree of diploidization and rearrangement. It is

probably the sole example of a palaeopolyploid in the Annonaceae (Morawetz & Waha, 1985).

In contrast to the extremely progressive and active evolution of the rather heterogeneous genera like *Annona* (Morawetz, 1984), the *Guatteria* -group which includes ca. 10% of all annonaceous

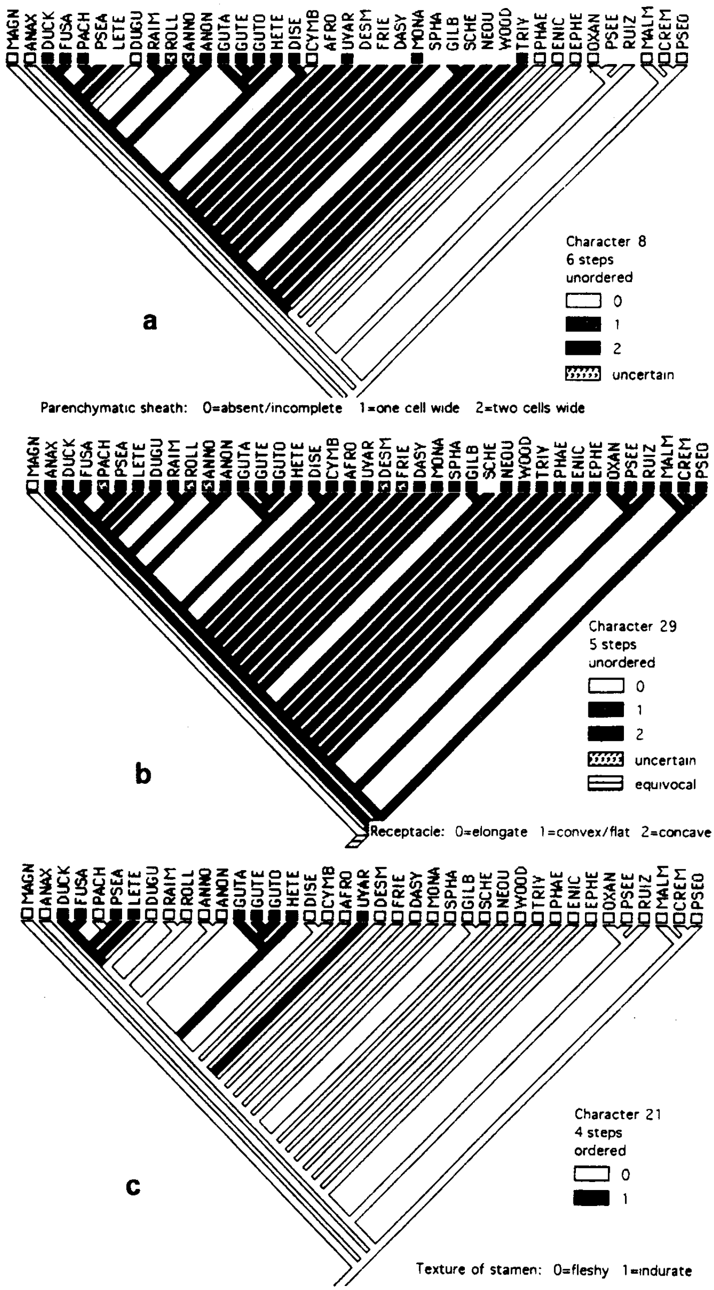

Fig. 5 Some character states linking the *Guatteria* -group with the (pseudo) syncarpous clade.

species, is very homogeneous. Morawetz & Waha (1985) suggested a rather slow, and more conservative evolving pattern. As argued from its monophyly and evolution pattern (Morawetz & Waha, 1985), the *Guatteria* -group is assumed to have been evolved from the common ancestor of Annonaceae in a very early time and has already undergone diversified speciation during the long evolutionary history. The first stage of its evolution seems to be more active and dramatic, which led to the generic divergence in the group. The second step is slower and more conservative, which causes its adaptation only to different ecological niches, and no more morphological differentiation events happened in this stage. From our analysis, the suggestion follows that the *Guatteria* -group has evolved relatively recently. The high number of species, indeed, points towards an active speciation.

The branching pattern within the *Guatteria* -group remains exactly the same in both the single most parsimonious tree and the consensus of one step longer trees, as well as in the phenogram. Both phylogenetic and phenetic analyses indicate that *Guatteria* (GUTA), *Guatteriella* (GUTE) and *Guatteriopsis* (GUTO) are very close together, while *Heteropetalum* (HETE) shows a sister relation with these three genera in the *Guatteria*- group.

Concerning its overall morphological similarities, the interpretations of our phenetic analyses (fig. 2, 3) agree broadly with the comment by van Setten & Koek-Noorman (1992) that the *Guatteria*-group has an intermediate position between the other apocarpous genera (like groups 4 and 10) and the (pseudo) syncarpous genera. The phylogenetic analyses, however, strongly suggest a sister relation of the group with the (pseudo) syncarpous clade (fig. 1). The cladogram also indicates that the *Guatteria*- group is the most derived one in the apocarpous grade because it possesses some rather derived characters and character states as mentioned above. Additionally, the karyotype of the *Guatteria*-group is certainly the most asymmetric one in Annonaceae, and possibly one of the most derived (Morawetz & Waha, 1985).

The sister group relation of the *Guatteria*- group with the (pseudo) syncarpous clade does not change in both strict and majority rule consensus trees of the one step longer trees (fig.4). Like the situation in other members of the apocarpous grade, such a sister relation is only supported by some synapormorphies that show more or less homoplasy. The *Guatteria*- group and most members of the (pseudo) syncarpous clade share a two cells wide parenchymatic sheath which occurs elsewhere only in *Monanthotaxis* (MONA) (fig.5a). The *Guatteria*- group also shares concave receptacles (fig.5b), indurate stamens (fig.5c), and complex histology of the primary vein with the *Duguetia* -group, a capitate stigma, and much reduced pollen exines with the *Annona* -group. The chromosome base number is another additional important character which may shed some light on the possible phylogenetic relationship of the *Guatteria*- group with the syncarpous *Annona*- group because both have the rare chromosome base number of 7. Another interesting clue for the possible link of the *Guatteria*-group and the (pseudo) syncarpous genera comes from the biochemical study by Cavé *et al*. (1989) who state that *Guatteria* and *Duguetia* seem to be exceptional among neotropical Annonaceae in the fact that they accumulate 6a, 7-trans-7-hydroxyaporphines which appear so far to be restricted to Annonaceae (Guinaudeau *et al*., 1975; 1988), and are mainly known as constituents of the African apocarpous genus

Polyalthia and the pseudosyncarpous genus *Pachypodanthium* (Leboeuf *et al*., 1982). Though the apocarpous genera and the (pseudo) syncarpous taxa have undergone drastic morphological divergence in the long evolutionary history and thus exhibit some strong dissimilarities, they can possibly be related to each other phylogenetically via the *Guatteria*-group as a link. This link may be explained by the so called "carpel fusion continuum" in Annonaceae (Schatz & Le Thomas, 1993). The (pseudo) syncarpous fruit resulted from the fusion of closed carpels along their lateral walls and it is therefore plurilocular. There is a continuum (even within a genus like *Duguetia*) in the degree of fusion of adjacent carpel walls, from only slight fusion at their base to almost complete fusion. In some cases, monocarps of an apocarpous fruit, that is, one in which the individual carpels are free all the way from tip to their base at the point of attachment to the receptacle, may be so tightly contiguous as to appear syncarpous (e.g., *Boutiquea*). Sinclair (1958) proposed a mechanism whereby sessile, or nearly so, carpels might "fuse" upon expansion if space were limiting. Space may be a limiting factor in conjunction with the contraction of the receptacle, as is the case of the aggregate fruits of *Kadsura* in Schisandraceae.

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References

Ariesteguieta L, 1969. In: Maguire B. & coll. eds, Botany of the Guayana Highlands. part 8. *Mem New York Bot Gard*, **18**(2): 43

Bakker M E, Gerritsen A F. 1992. Oil and mucilage cells in *Annona* (Annonaceae) and their systematic significance. *Blumea* , **36**: 411 ~ 438

Ban N T, 1975. Notes on the genus *Dasymaschalon* (Hook.f. et Thoms.) Dalle Torre et Harms (Annonaceae). *Bot Zurn*, **60**: 223 ~ 233

Cavé A, Leboeuf M, Cassels B K, 1989. Alkaloids from *Guatteria*. *The Alkaloids* , **35**: 1 ~ 73

Diels L. 1912. Die Annonaceen von Papuasien. *Bot Jahrb Syst*, **49**: 152 ~ 153

Doyle J A, Le Thomas A, 1994. Cladistic analysis and pollen evolution in Annonaceae. *Acta Bot Gallica*, **141**(2): 149 ~ 170

Doyle J A, Le Thomas A, 1995. Evolution of pollen characters and relationship of African Annonaceae: Implications of a cladistic analysis. *Publ Occas CIFEG*, **31**: 241 ~ 254

Ehrendorfer F, Krendl F, Habeler E *et al*, 1968. Chromosome numbers and evolution in primitive Angiosperms. *Taxon*, **17**: 337 ~ 353

Finet A, Gagnepain F, 1906. Contribution à l'étude de la flore de l'Asie orientale. *Bull Soc Bot France*, **53**(4): 55 ~ 170

Fries R E, 1934. Revision der Arten einiger Annonaceen- Gattungen. III. *Acta Horti Berg*, **12**(1): 106

Fries R E, 1959. Annonaceae. In: Engler A, Prantl K, ed. Die Natürlichen Pflanzenfamilien, 2nd ed., Berlin: Duncker & Humblot, 1 ~ 171

Gottsberger G, 1974. The structure and function of the primitive Angiosperm flower. A discussion. *Acta Bot Neerl*, **23**: 461 ~ 471

Guinaudeau H, Leboeuf M, Cavé A, 1975. Aporphine alkaloids. *Lloydia*, **38**(4): 275 ~ 324

Guinaudeau H, Leboeuf M, Cavé A, 1988. Aporphinoid alkanoids, IV. *J Nat Prod*, **51**(3): 389 ~ 474

Hennig W, 1966. Phylogenetic systematics. Urbana: Univ. Illinois Press

Heusden E C H van, 1992. Flowers of Annonaceae: Morphology, classification and evolution. *Blumea* Suppl, **7**: 1 ~ 218

Huber H, 1985. Annonaceae. In: Dassanayake M D ed. A revised handbook to the flora of Ceylon. New Delhi: Amerind Publishing, 1 ~ 75

Humphries C J, Funk V A, 1984. Cladistic methodology. In: Heywood V, Moore H, ed. Current concepts in plant taxonomy, London: Academic Press, 323 ~ 362

Hutchinson J, 1964. The genera of flowering plants. Oxford: Clarendon Press

Hutchinson J, 1969. Evolution and phylogeny of flowering plants. New York, London: Academic Press, 1 ~ 24

Jovet-Ast S, 1942. Recherches sur les Annonacées d'Indochine. Anatomie foliaire. Répartition géographique. *Mém Mus Natl Hist Nat*, **16**:125 ~ 308

Kessler P J A, 1993. Annonaceae. In: Kubitzki K, ed. The families and genera of vascular plants. Berlin: Springer-Verlag, II: 93 ~ 129

King G, 1893. The Annonaceae of British India. *Ann Roy Bot Gard*, **4**: 1 ~ 169

Klucking E P, 1986. Leaf venation patterns. Vol. 1. Annonaceae. Berlin: J. Cramer

Koek-Noorman J, Setten A K van, Zuilen C M van, 1997. Studies in Annonaceae XXVI. Flower and fruit morphology in Annonaceae. Their contribution to patterns in cluster analysis. *Bot Jahrb Syst* , **119**:1 ~ 18

Leboeuf M, Cavé A, Bhaumik P K, *et al*, 1982. The phytochemistry of the Annonaceae. *Phytochemistry*, **21**(12): 2783 ~ 2813

Leins P, Erbar C, 1996. Early floral developmental studies in Annonaceae. In: Morawetz, W, Winkler H, ed. Reproductive morphology in Annonaceae. Wien: Österreichische Akademie der Wissenschaften, 1 ~ 28

Le Thomas A, 1969. Annonacées. Flore du Gabon, no. 16. Paris: Muséum national d'Histoire naturelle

Le Thomas A, 1980 ~ 1981. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive Angiosperms. *Pollen & Spores*, **22**: 267 ~ 342, **23**: 5 ~ 36

Le Thomas A, Lugardon B, 1974. Quelques types de structure grenue dans l'ectexine de pollens simples d'Annonacées. *Compt Rend Hebd Séances Acad Sci*, **278**: 1187 ~ 1190

Le Thomas A, Morawetz W, Waha M, 1986. Pollen of palaeo- and neotropical Annonaceae: definition of the aperture by morphological and functional characters. In: Blackmore S, Ferguson I K, ed. Pollen and spores: form and function. London: Academic Press, 375 ~ 388

Maas P J M, Heusden E C H van, Koek-Noorman J, *et al*, 1983. Synoptical key to the neotropical genera in Annonaceae. *Meded Bot Mus Herb Rijksuniv Utrecht*, **516**: 1 ~ 11

Maas P J M, Westra& L Y Th, 1984. Studies in Annonaceae II. A monograph of the genus *Anaxagorea* A. St. Hil., Part 1. *Bot Jahrb Syst*, **105**: 73 ~ 134

Maddison W P, Donoghue M J, Maddison D R, 1984. Outgroup analysis and parsimony. *Syst Zool*, **33**: 83 ~ 103

Maddison W P, Maddison D R, 1992. MacClade: analysis of phylogeny and character evolution, version 3. Massachusetts: Sinauer Associates, Sunderland

Merrill E D, 1922. New or noteworthy Bornean plants. *J Straits Branch Roy Asiat Soc*, **85**: 174 ~ 189

Morawetz W, 1984. Karyologie, Okologie und Evolution der Gattung *Annona* in Pernambuco, Brasilien. *Flora*, **175**: 335 ~ 347

Morawetz W, 1986. Remarks on karyological differentiation patterns in tropical woody plants. *Pl Syst Evol*, **152**: 49 ~ 100

Morawetz W, 1988. Karyosystematics and evolution of Australian Annonaceae as compared with Eupomatiaceae, Himantandraceae, and Austrobaileyaceae. *Pl Syst Evol*, **159**: 49 ~ 79

Morawetz W, Maas P J M, 1984. Notes on the systematics of the Amazonian genus *Guatteriella* (Annonaceae). *Pl Syst Evol*, **148**: 19 ~ 23

Morawetz W, Waha M, 1985. A new pollen type, C-banded and fluorochrome counterstained chromosomes, and evolution in *Guatteria* and related genera (Annonaceae). *Pl Syst Evol*, **150**: 119 ~ 141

Nooteboom H P, 1985. Notes on Magnoliaceae, with a revision of *Pachylarnax* and *Elmerrillia* and the Malesian species of *Manglietia* and *Michelia*. *Blumea*, **31**: 65 ~ 121

Nooteboom H P, 1993. Magnoliaceae. In: Kubitzki K, ed. The families and genera of vascular plants. Berlin: Springer-Verlag, II: 391 ~ 401

Pierre L, 1880. Flore forestière de la Cochinchine. Paris: Octave Doin, 17

Rohlf F J, 1994. NTSYS-pc version 1.80: Numerical taxonomy and multivariate analysis System. Stony Brook, New York: State University of New York

Sanderson M J, Donoghue M J, 1989. Patterns of variation in levels of homoplasy. *Evolution*, **43**: 1781 ~ 1795

Schatz G E, Le Thomas A, 1993. Annonaceae: A primitive dicot family with an ancient center in Africa-South America. In: Goldblatt P, ed. Biological relationship between Africa and South America. New Haven: Yale University Press, 86 ~ 104

Scheffer R H C C, 1885. Sur quelques plantes nouvelles ou peu connues de L'Archipel Indien (Annonaceae). *Ann Jard Bot Buitenzorg*, **2**: 1 ~ 31

Setten A K van, Koek-Noorman J, 1986. Studies in Annonaceae VI. A leaf anatomical survey of genera of Annonaceae in the Neotropics. *Bot Jahrb Syst*, **108**: 17 ~ 50

Setten A K van, Koek-Noorman J, 1992. Studies in Annonaceae XVII. Fruits and seeds of Annonaceae. Morphology and its significance for classification and identification. *Bibliotheca Bot*, **142**: 1 ~ 101

Setten A K van, Maas P J M, 1990. Studies in Annonaceae. XIV. Index to generic names of Annonaceae. *Taxon*, **39**: 675 ~ 690

Sinclair J, 1955. The revision of the Malayan Annonaceae. *Gard Bull Straits Settl*, **14**: 149 ~ 516

Sinclair J, 1958. *Ararocarpus*: a monstrosity. *Gard Bull Straits Settl*, **17**: 93 ~ 95

Sugiyama M, 1979. A comparative study of nodal anatomy in the Magnoliales based on the vascular system in the node-leaf continuum. *J Fac Sci Univ Tokyo* (Bot ser), **12**: 199 ~ 279

Swofford D L, 1993. Phylogenetic analysis using parsimony (PAUP), version 3.1.1 for Apple/Macintosh, distributed by the Illinois Natural History Survey. Illinois: Champaign

Uphof J C Th, 1959. Eupomatiaceae, Myristicaceae. In: Engler A, Prantl K ed. Die Natürlichen Pflanzenfamilien, 2nd ed. Berlin: Duncker & Humblot, Band 17a: 173 ~ 220

Verdcourt B, 1971. Annonaceae. In: Milne-Redhead E, Polhill R M, ed. Flora of tropical East Africa. Richmond: Royal Botanical Gardens, Kew, **17**: 1 ~ 131

Walker J W, 1971a. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. *Contr Gray Herb*, **202**: 1 ~ 132

Walker J W, 1971b. Unique type of Angiosperm pollen from the family Annonaceae. *Science*, **172**: 565 ~ 567

Walker J W, 1976. Evolutionary significance of the exine in the pollen of primitive angiosperms. In: Ferguson I K, Muller J ed. The evolutionary significance of the exine. London: Academic Press, 1112 ~ 1137

Watrous L, Wheeler Q, 1981. The out-group comparison method of character analysis. *Syst Zool*, **30**: 1 ~ 11

Welle B J H ter, 1984. Variation and diversity in the Annonaceae. In: Sudo S, ed. Proceeding of Pacific regional wood anatomy conference. Tsukuba: Pacific regional wood anatomy conference publish, 144 ~ 146

Westra L Y Th, 1995. Studies in Annonaceae XXIV. A taxonomic revision of *Raimondia* Safford. *Bot Jahrb Syst*, **117**(3): 273 ~ 297

Zuilen C M van, 1996. Patterns and affinities in the Duguetia alliance (Annonaceae): Molecular and morphological studies. Utrecht: University of Utrecht, 123 ~ 129